

SILVABESTIUS GEN. NOV., A PRIMITIVE ZYGOMATURINE (MARSUPIALIA, DIPROTODONTIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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A new genus and two new species of primitive Oligo-Miocene zygomaturines are described from Riversleigh, northwestern Queensland. A maxillary fragment described by Tedford as palorchestine (Marsupialia: Palorchestidae) is referred to *Silvabestius*, and is intermediate between *S. michaelbirti* sp. nov. and *S. johnnilandi* sp. nov. Trends in premolar morphology within the genus support Stirton et al.'s proposal that zygomaturines arose from primitive diprotodontine-like forms in which the parastyle on P³ was less developed. The tricuspid P³ of *S. michaelbirti* is intermediate between the bicuspid P³ of primitive diprotodontines and the more typical quadricuspid P³ of *S. johnnilandi*. Cladistic analysis of the Zygomaturinae, based largely on the upper third premolar, is compared with previous analyses.

□ Zygomaturinae, *Silvabestius*, Riversleigh, Oligocene, Miocene.

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Tedford (1967) described Palorchestinae gen. and sp. indet., a right maxillary fragment containing P³-M¹ and the anterior half of M² from Site D, Riversleigh, northwestern Queensland. This assignment was based on plesiomorphic features that were at the time otherwise only known in primitive palorchestids such as *Ngapakaldia* and *Pitikantia*. Tedford (1967) did, however, note enlargement of the parastylar region, a low parastyle and a more extensive posterolingual cingular shelf in P³ that appeared to anticipate development of the quadricuspid premolars of primitive zygomaturines. These features were also noted by Hand et al. (1993b) who, in light of primitive zygomaturines from northern Australia (*Nimbadon* Hand et al., 1993a; *Alkwertatherium* Murray, 1990b), Hand et al. (1993b), referred the D-site specimen to the Zygomaturinae.

Two perfectly preserved crania of the primitive zygomaturine diprotodontid, *Silvabestius johnnilandi* sp. nov. were collected at VIP Site in 1989 and a complete skull of *Silvabestius michaelbirti* sp. nov. was recovered from Hiatus Site in 1992. Both species show striking similarities in dental morphology to Tedford's Site D maxillary fragment.

This paper describes these new species and provides a phylogenetic analysis of the Zygomaturinae based on dental features. Particular attention focuses on P³, which tooth appears most useful in diprotodontoid phylogenetic analyses (Stirton et al., 1967).

Material is deposited in the palaeontological collection of the Queensland Museum (QMF)

and the palaeontological collection of the Bureau of Mineral Resources, Canberra (CPC). Cusp nomenclature follows Archer (1984) and Riech et al. (1978) except that what was then understood to be the hypocone of upper molars is now accepted to be the metaconule following Tedford & Woodburne (1987). Molar homology follows Luckett (1993). Premolar homology follows Flower (1867). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family DIPROTODONTIDAE Gill, 1872
Subfamily ZYGOMATURINAE Stirton,
Woodburne & Plane, 1967

Silvabestius gen. nov.

TYPE SPECIES. *Silvabestius johnnilandi* sp. nov.

OTHER SPECIES. *Silvabestius michaelbirti* sp. nov., Palorchestinae gen. and sp. indet. of Tedford (1967) (= *Silvabestius* sp. herein).

DIAGNOSIS. *Silvabestius* differs from other zygomaturines in the following combination of features: small parastyle on P³; absence of a deep trench separating parastyle from parametacone base on P³; absence of a well-developed lingual margin on upper molars; presence of upper canines (except *Neohelos*); absent or small

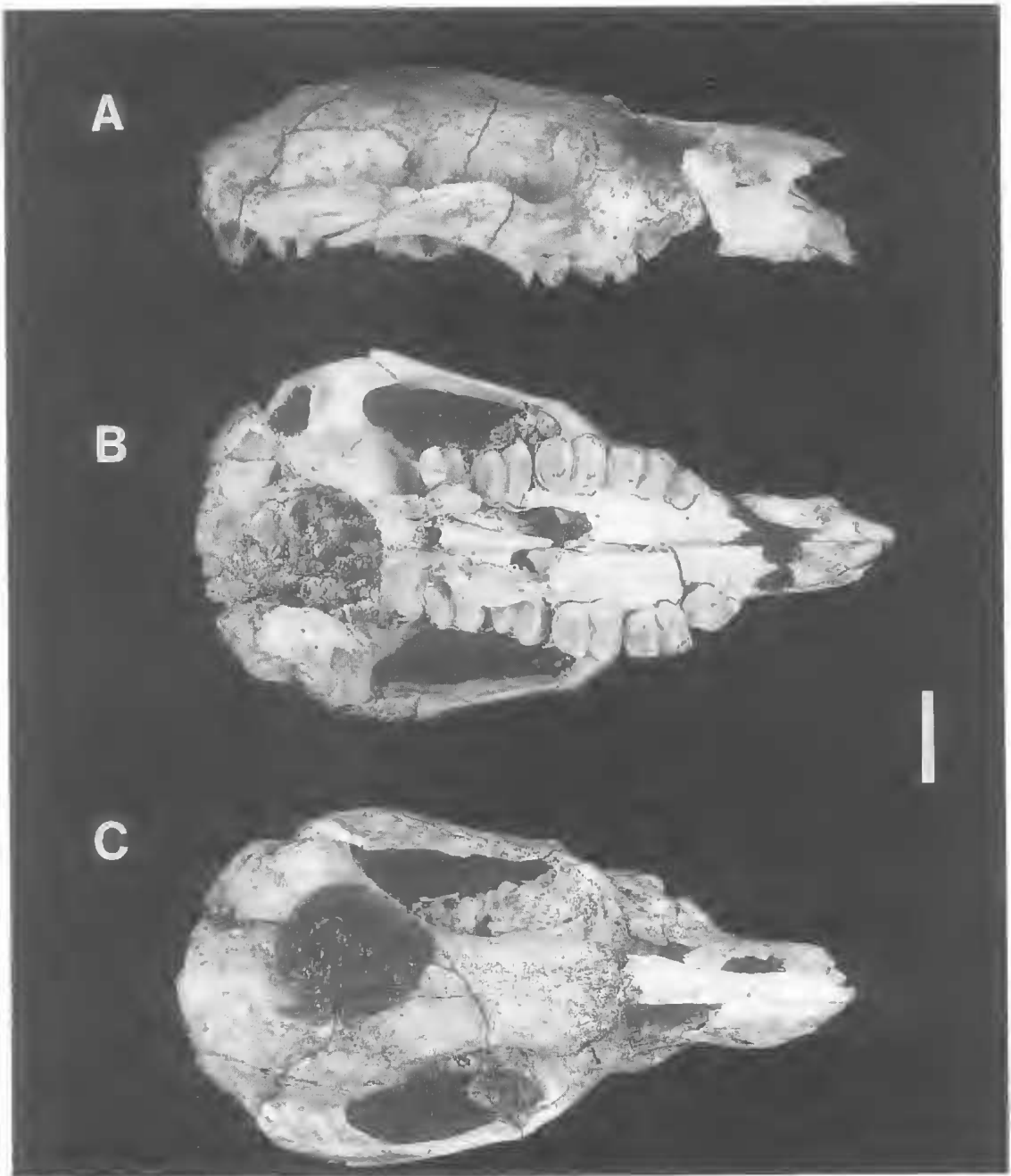


FIG. 1. *Silwabestius johnnilandi* gen. et sp. nov., holotype, QMF30504. A, right lateral view, B, ventral view, C, dorsal view. Bar = 20mm.

hypocone on P³ (except *Alkwertatherium webbi*); more anteriorly convex upper molar lochs (except for *Nimbadon*). It is distinguished from other zygomaturines except *Raemotherium yatkolai*

and *Nimbadon* by: its small size; molar gradient that does not appreciably increase posteriorly. It is distinguished from other zygomaturines except *Nimbadon* and *Neohelos* by: the anterobuccal



FIG. 2. *Silwabestius johnnilandi* gen. et sp. nov., holotype, QMF30504. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

blade from the parametacone on P^3 ; absence of a well-developed buccal cingulum or metastyle on P^3 . It can be distinguished from other zygomaturines except *Neohelos*, *Nimbadon* and *A. webbi* by an undivided parametacone on P^3 .

ETYMOLOGY. Latin *silva*, forest and *bestia*, beast; for its inferred habitat; masculine.

***Silwabestius johnnilandi* sp. nov.**
(Figs 1-6)

MATERIAL. Holotype QMF30504, a juvenile skull and associated mandible with completely unworn left and right cheek tooth rows. The basicranium, palate and nasals are incomplete. Both dentaries are missing the coronoid process. I^{2-3} is missing on each side. P^3 and M^{3-4} on each side were unerupted at the time of



FIG. 3. *Silvestrius johnnilandi* gen. et sp. nov., right dentary of holotype QMF30504. Occlusal stereopair. Bar = 10mm.

death. Paratype QMF30505, a virtually complete adult skull; its frontals are broken and slightly depressed; a large fracture runs diagonally from the left orbit to the dorsal surface of the premaxilla and continues ventrally through the right canine alveolus and onto the palate. The right palatine bone is fractured and depressed. The left mastoid/paroccipital process is broken. The supra-occipital is incomplete. Both types from VIP Site which is 3m below D Site; the latter contains diprotodontoids some of which belong to genera that occur in the late Oligocene in the Etadunna Formation (Woodburne et al., 1994) and thus we assign VIP Site to the late Oligocene.

Although a juvenile the holotype has perfectly unworn dentition which maximises information about crown morphology and both the skull and lower jaws, whereas the paratype is only a skull.

ETYMOLOGY. For Professor John Niland, Vice Chancellor of the University of New South Wales who

has been a strong supporter of the Riversleigh Project and helped collect at Riversleigh.

RELATIONSHIP OF THE HOLOTYPE TO THE PARATYPE. We conclude that QMF30504 was a dependent pouch-young living on its mother's (QMF30505) milk because: 1) both specimens were in the same deposit, within 1m of each other; 2) the lack of wear on the teeth of QMF30504 most of which were still erupting and the lack of fusion of any of its cranial bones; 3) when the upper and lower cheek teeth of the juvenile are brought into occlusion, the upper and lower incisors do not meet, but are separated by a gap of approximately 6 mm, a gap appropriate to suit a mother's nipple. 4) LI^3 of the adult skull, which was thought to be missing, was found adjacent to the nose of the juvenile skull suggesting that the adult and juvenile died nose to nose, suggesting an emotional relationship.

DIAGNOSIS. This species differs from *S. michaelbirti* in the following combination of features: it is much larger; it has an expanded parastylar region on P^3 and more distinct parastyle; it has a more posterior parametacone on P^3 ; it has a larger protocone on P^3 that is also

more distinctly separated from the base of the parametacone by a deep fissure; it has a small but distinct hypocone on P^3 ; and it has less steeply sloping surfaces on the protoloph and metalophs of M^{1-4} .

DESCRIPTION. Upper incisors. L and RI^1 in the Holotype; L , RI^{1-2} and LI^3 in the Paratype. I^1 large, curved, with a thick, rounded base tapering to its tip. Enamel confined to the anterolateral surfaces and the upper third of the distal surface. L and RI^1 convergent at their tips. I^2 small, sub-ovate, tapering anteriorly, with narrow anterior tip contacting the posterolateral face of I^1 , with crown dominated by a large, ovate wear facet. I^3 posterior and slightly lateral to I^2 , smaller than I^2 , with a triangular occlusal surface, with apex oriented anteromedially, with a wear facet on most of the occlusal surface.

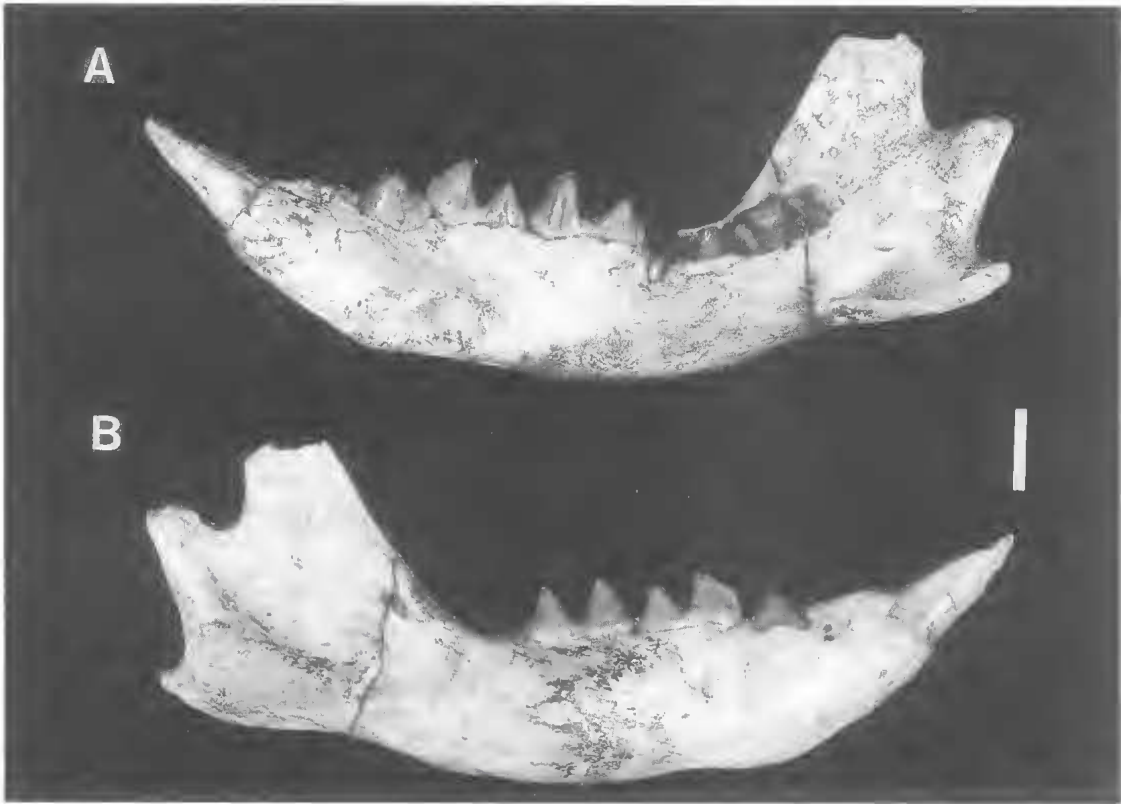


FIG. 4. *Silwabestius johnnlandi* gen. et sp. nov., right dentary of holotype QMF30504. A, lingual view. B, buccal view. Bar = 10mm.

Upper canines. Adult skull with small canine alveolus just posterior to the premaxillary/maxillary suture; obscured in the juvenile skull.

P³. Four cusps: a large parametacone; a well-developed protocone; a small distinct parastyle; and a poorly-developed hypocone. Widest across the protocone. Emargination between the bases of the protocone and lobate parastylar region defining the anterior and posterior moieties. Paratype premolar proportionately longer than that of the Holotype and the anterior and posterior moieties are more distinct. Large, undivided parametacone the tallest cusp on the premolar, situated along the midline of the tooth, slightly posterior to its transverse axis. Protocone large, lingually opposite the parametacone. Hypocone small but distinct, on the lingual cingulum at the posterolingual base of the protocone. Paratype P³ with extremely reduced and non-cusped hypocone.

Parametacone pyramidal in occlusal view with steep buccal, anterolingual and posterolingual faces. Each face defined by a distinct blade: an

anterior preparametacrasta, a posterior postparametacrasta and an anterolingually directed blade. Preparametacrasta linear, extending anteriorly (and slightly buccally) from the parametacone apex, continuous with a short, arcuate, posterobuccal blade from the parastyle. The anterolingually-oriented blade descending the anterolingual face of the parametacone, terminating in the fissure that separates the bases of the protocone and parametacone, just prior to meeting its counterpart, a short, linear, anterobuccally-directed protocone crest. A similar condition is found in *Nimbadon lavarackorum* (Hand et al., 1993a) and some *Neohelos* specimens from the Oligocene-Miocene of Riversleigh. In the paratype, the anterolingual parametacone blade is continuous with the anterolingual cingulum, a feature previously regarded as an autapomorphy of *Nimbadon* (Hand et al., 1993a). A slight swelling at the junction of the anterolingual blade and the lingual cingulum may represent a small protostyle.

TABLE 1. Measurements (mm) of *Silvabestius*. H=Height of crown; A/P=anterior-posterior length; Th=Thickness; W=width; IMP° = implantation angle; #=broken specimen; *=dimensions of alveoli.

A. I ¹ MEASUREMENTS					
Species	No	Side	H	A/P	W
johnniliandi	QMF 30504	L	7.1	-	6.5
		R	8.3	-	6.7
	QMF 30505	L	16.0#	8.7	6.9
		R	20.1#	8.3	6.9
michaelbirti	QMF 20493	L	18.9#	7.2	7.0
		R	18.3#	8.1	6.8
B. I ² MEASUREMENTS					
johnniliandi	QMF 30505	L	5.4	6.4	5.0
		R	5.4	6.3	5.1
michaelbirti	QMF 20493	L	-	5.9*	4.5*
		R	5.7	6.0	4.7
C. I ³ MEASUREMENTS					
johnniliandi	QMF 30505	L	4.7	5.3	4.1
		R	-	-	-
michaelbirti	QMF 20493	L	-	5.3*	4.8*
		R	-	5.2*	4.3*
D. UPPER CANINE MEASUREMENTS					
johnniliandi	QMF 30505	L	-	3.0*	2.2*
		R	-	3.2*	2.1*
michaelbirti	QMF 20493	L	6.3	5.1	3.5
		R	6.2	5.2	3.5
E. LOWER INCISOR MEASUREMENTS					
			Th	W	IMP°
johnniliandi	QMF 30504	L	7.0	4.7	30°
		R	8.1	4.6	30°

Postparametacrista well-developed, blade-like, continuous with the posterolingual cingulum.

Small, erect parastyle at the anterolingual corner, slightly buccal to the tooth margin, dominated by a distinct, arcuate blade continuous with the preparametacrista. Parastyle in paratype reduced to a slight swelling at the anterior tip of the preparametacrista. Short, ill-defined, anterolingual parastyle crest continuous with the anterolingual cingulum. Shallow anterolingual basin between the bases of the parastyle, parametacone and protocone, better defined in holotype RP³, but extremely shallow on the crown of the paratype.

Short, posteriorly-directed, apical protocone crest terminating 1/3 the way down its posterior surface. Two short, linear crests extending from the apex of the hypocone; one extending anteriorly and terminating at the posterior base of the protocone; other extending posteriorly, continu-

ous with the posterolingual cingulum. Buccal cingulum poorly-developed in the Holotype. Buccal surface of the parametacone with uniform, steep gradient to the base of the tooth crown. Well-developed buccal cingular shelf in the Paratype.

Upper molars. Proportionately similar to *Nimbadon whitelawi* from the mid-Miocene Bullock Creek Local Fauna (Hand et al., 1993a).

M¹. Sub-rectangular, low-crowned, transversely-bilophodont, with an anterior protoloph and posterior metaloph. Protoloph and metaloph short, anteriorly-convex crests, former slightly more arcuate than the latter; protoloph consisting of a buccal paracone and a lingual protocone; metaloph consisting of a buccal metacone and a lingual metaconule; metaconule the tallest cusp, followed by the paracone, metacone, then protocone. Parastyle small, at the anterobuccal end of the anterior cingulum, connected to an anterior paraconal crest by a short, posteriorly-oriented blade. Paratype parastyle poorly developed, slight swelling at the junction of the anterior paraconal crest and the anterior cingulum. Postmetacrista distinct, extending posteriorly from the metacone apex, continuous with the posterior cingulum. Metastyle a slight swelling at the posterobuccal margin, most reduced in the Paratype. Posterior cingulum terminating at the posterolingual base of the metaconule. Lingual cingulum in Holotype poorly developed, in Paratype short, crescentic, joining bases of the protocone and metaconule, blocking the lingual exit of the interloph valley. Short, indistinct, postparaconal crest descending the posterior face of the paracone, terminating in the interloph valley, before meeting its counterpart, an indistinct premetacrista. Short, linear, apical blade on the metaconule. Paratype with facets extending posterobuccally from the apices of the protocone and metaconule, fading down the posterior flanks of their respective cusps.

M²⁻⁴. Similar to M¹ except: Larger, proportionately wider anteriorly, with molars trapezoidal in occlusal view; paracone tallest cusp, protoloph higher than metaloph; parastyle and metastyle and their associated crests extremely reduced, as are the postparaconal crest and the premetacrista; lophs relatively longer, with protoloph longer than the metaloph, becoming more anteriorly convex in the more posterior molars; metaloph severely reduced, more obliquely oriented relative to the protoloph, with posterior moiety severely reduced. Molars increasing in size through M¹⁻², decreasing through M³⁻⁴. M¹ reduced, lack-

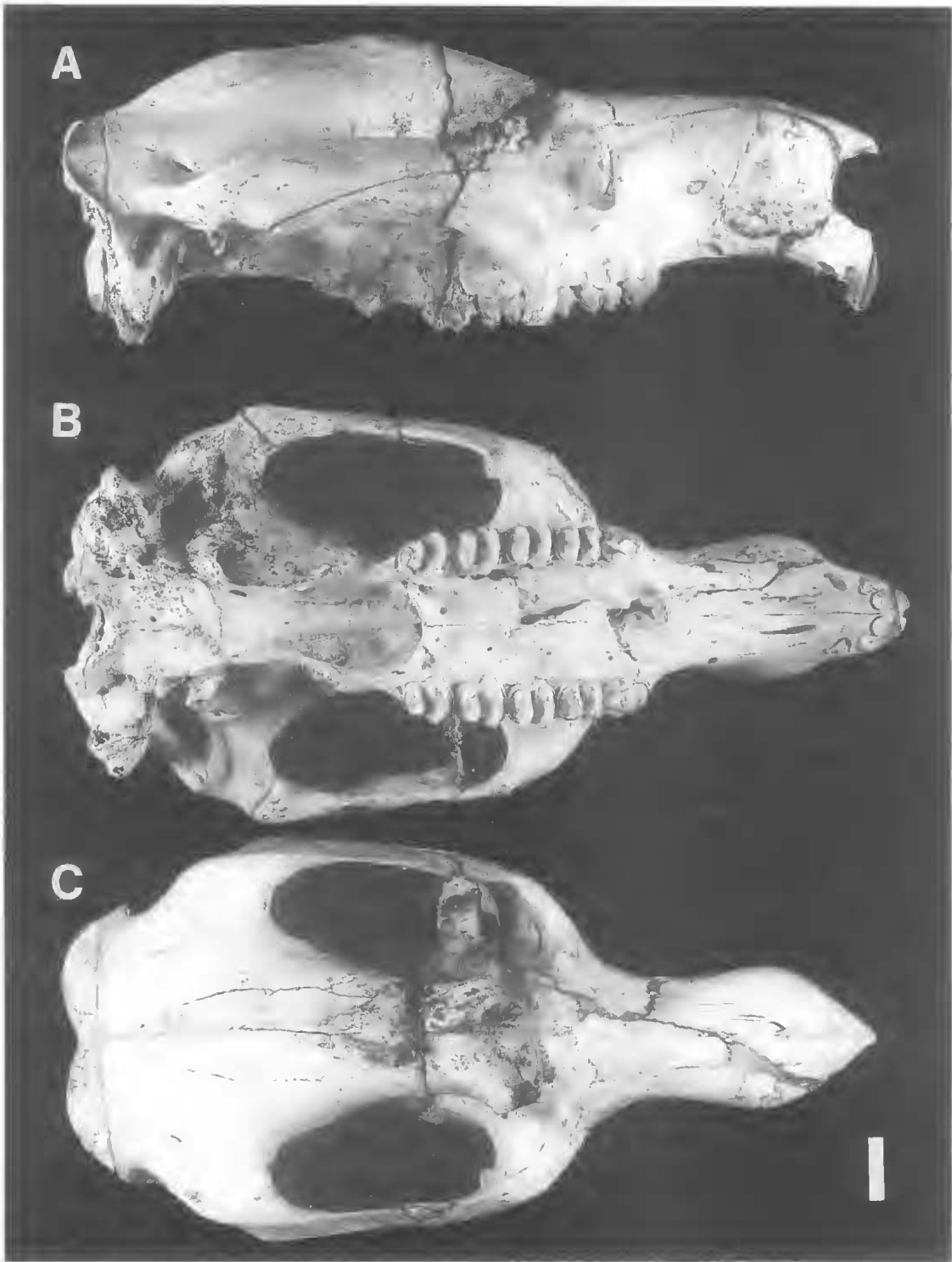


FIG.5. *Silvestrius johnnili* gen. et sp. nov., paratype QMF30505. A, right lateral view. B, ventral view. C, dorsal view. Bar = 20mm.

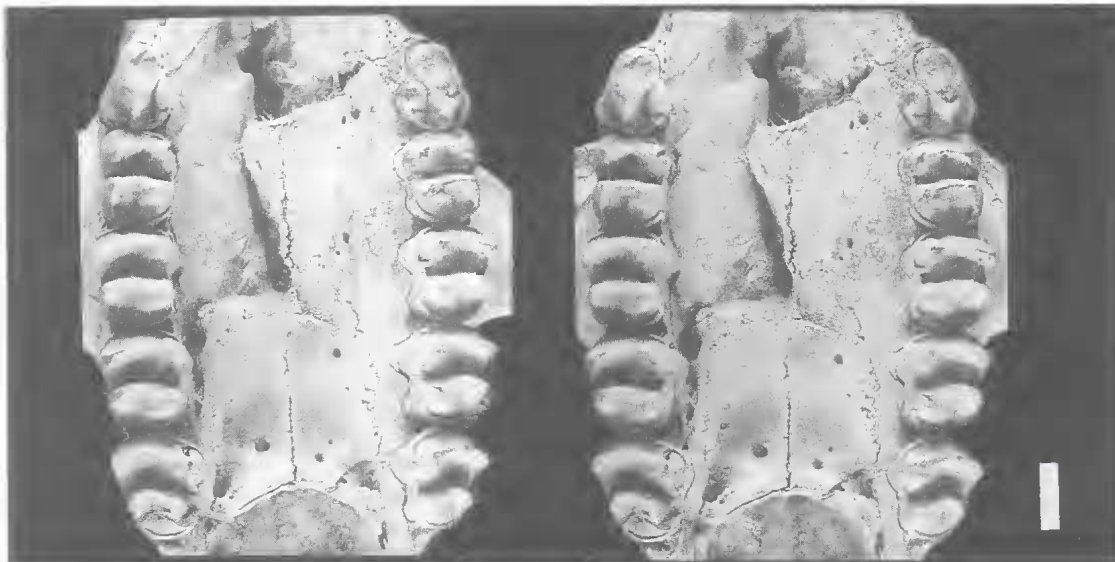


FIG. 6. *Silvestrius johnniliandi* gen. et sp. nov., paratype, QMF30505. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

ing enamel. Adult cheektooth row with an increasing molar gradient from M^1 to M^4 .

Lower dentition. A single pair of lanceolate, procumbent lower incisors in the Holotype. Enamel only on the lateral and ventral surfaces of the crown. A longitudinal groove occupying the internal dorsal surface, extending from the base of the incisor to the tip, approximately 2mm below and lingual to the dorsolateral tooth margin.

P_3 . Short, subovate, longer than wide, tapering anteriorly, dominated by a high, steep protoconid, with a short, steep, arcuate blade extending pos-

teriorly from the protoconid apex, terminating in a small cuspid on the posterior cingulid. A poorly defined crest descending the anterior face of the protoconid, terminating in a slight swelling at the anterior tooth margin. Posterobuccal cingulum poorly developed. Lingual cingulum curving around the posterolingual tooth margin, from the apex of the posteromedial cuspid to a point midway between the protoconid apex and posterior tooth margin. A vertical flanking crest descending the steep buccal face of the protoconid to a point just anterior to the terminus of the lingual cingulum.

TABLE 2. Measurements (mm) of *Silvestrius*. L=length; AW=anterior width; PW=posterior width; *estimates.

A. UPPER CHEEK DENTITION																
Species	No.	Side	P3		M1			M2			M3			M4		
			L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
<i>johnniliandi</i>	QMF 30504	L	12.2	10.5	13.5	10.4	10.2	14.8	12.4	11.2	14.5	11.8	-	12.0	11.4	9.0
		R	11.7	10.7	13.6	10.6	10.2	14.5	12.5	11.4	14.3	12.9	10.8	11.5	11.8	9.1
	QMF 30505	L	13.1	11.3	14.4	11.9	11.5	14.7	13.2	11.8	15.2	13.2	11.4	15.3	12.8	9.8
		R	12.6	10.9	13.6	11.7	11.4	15.0	12.3	11.2	15.3	12.8	10.8	15.5	14.1	10.2
<i>michaelbirti</i>	QMF 20493	L	9.6	7.5*	10.4*	9.4*	9.0*	12.9	10.1*	9.2*	12.0	11.4*	9.8*	12.0	10.2	8.2
		R	9.6	8.3	11.3	9.7	9.3	11.3	10.4	9.6	11.3	10.3	8.7	11.3	10.2	8.1
sp.	CPC 7337	R	12.5	9.3	13.5	10.3	10.7	-	12.4	-						
B. LOWER CHEEK DENTITION																
<i>johnniliandi</i>	QMF 30504	L	10.8	7.1	13.5	8.1	8.9	14.6	9.6	10.3	14.6	11.3	9.0	12.7	-	9.2
		R	10.3	6.6	13.7	8.1	8.7	15.3	9.6	9.9	13.7	11.0	10.2	12.9	10.8	9.3

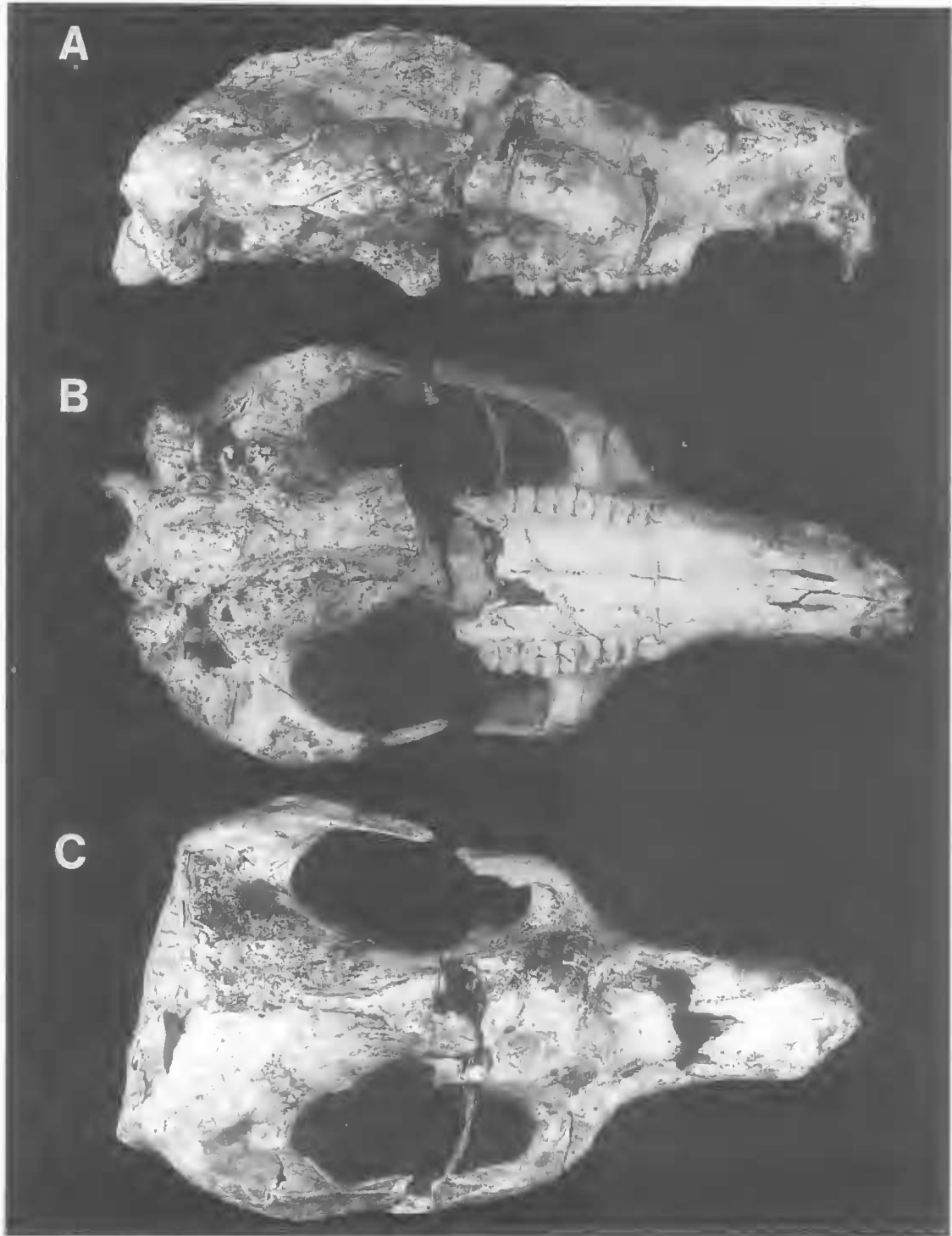


FIG. 7. *Silwabestius michaelbirti* sp. nov., holotype, QMF20493. A, right lateral view. B, ventral view. C, dorsal view. Bar = 20mm.

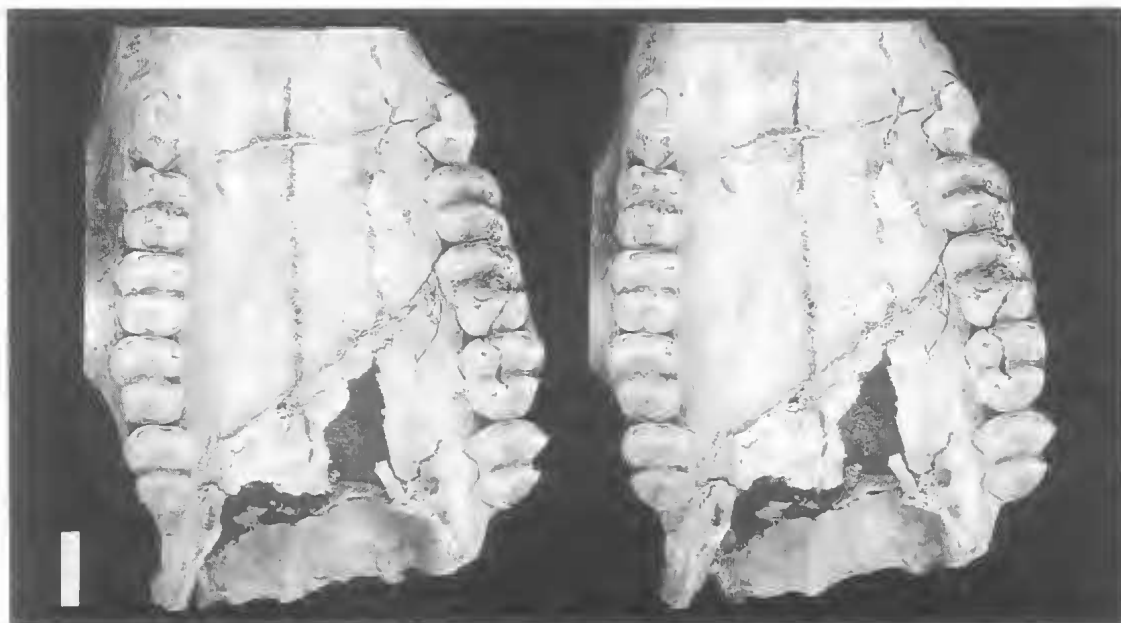


FIG. 8. *Silwabestius michaelbirti* sp. nov., holotype, QMF20493. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

M₁. Subrectangular, anteriorly-tapering, transversely bilophodont. Anterior protolophid short, steep, high, running parallel to a steep, low, posterior hypolophid. Protoconid higher than metaconid; entoconid higher than the hypoconid. Paracristid anteriorly directed, blade-like, linking the protoconid to the anterior cingulum, slightly buccally convex. Anterior cingulum curving lingually and downward, to the base of the crown, meeting a relatively indistinct preprotocristid. Deep anterior basin defined by the junction of these crests and the anterior base of the protoconid. A short, vague crest fading down the posterobuccal base of the protoconid. Similar, better-defined crest fading down the posterior face of the metaconid. A well-developed, anterobuccally oriented prehypocristid terminating approximately 1/3 the way down the anterior face of the hypolophid. Lingual cingulum discontinuous, comprised of 2 ridges extending postrobuccally and posterolingually from the bases of the protoconid and hypoconid, respectively, with both ridges terminating just short of meeting each other in the interlophid valley. Similar short ridge at the posterobuccal base of the metaconid. Posterior cingulum short, not extending around the bases of the entoconid and hypoconid. Transverse valley U-shaped in lingual view.

M₂. Similar to M₁ in all aspects except: slightly larger; protolophid subequal to its hypolophid; protolophid and hypolophid transversely wider; paracristid and prehypocristid extremely reduced; all ridges associated with the main cuspids reduced; anterior face of the protolophid steeper; anterior cingulum better-developed; anterior basin absent.

M₃₋₄. Only partially erupted, similar to M₂ in all aspects except: M₃ less elongate, but wider than M₂; M₄ reduced relative to M₂₋₃; hypolophid reduced relative to the protolophid, slightly offset relative to the protolophid, more posteriorly convex; interlophid valley more open and broadly U-shaped.

REMARKS. Variation in the hypocone is common among Oligo-Miocene zygomaticurines. In fact, hypocone-less variants have been recorded for species of *Neohelos* (Peter Murray pers. comm.) and *Nimbadon* (Hand et al., 1993a). The development of a hypocone has, in the past, served as a synapomorphy of the Zygomaticurinae. We have used this feature in the phylogenetic systematic analysis presented below because, although variable, it is generally a good indicator of phylogenetic relationships.

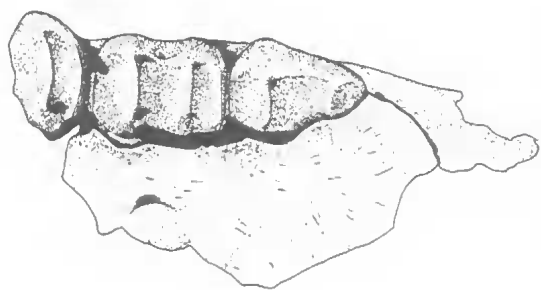


FIG. 9. *Silwabestius* sp., CPC7337. Occlusal view of right maxillary fragment with P³-M² from Site D Locality, Riversleigh. (After Tedford, 1967).

***Silwabestius michaelbirti* sp. nov.**
(Figs 7-8)

MATERIAL. Holotype QMF20493, a relatively complete cranium from late Oligocene Hiatus (South) Site (Creaser, 1997) with left and right cheek tooth rows; a longitudinal fracture runs through LM¹⁻³; RM¹ is fractured diagonally from the anterolingual tooth corner to the posterobuccal tooth corner; L and RI¹ are present

TABLE 3. Character state polarities for selected zygomaturine genera using species of *Ngapakaldia* (Palorchestidae) as an outgroup. A=absent; P=present; S=small; D=distinct; W=weak; ST=strong; SQ=square; R=reduced; ==equal or sub-equal. PLESIO=plesiomorphic; APO=apomorphic.

CHARACTER	PLESIO-	APO-
1. Parastyle development on P ³	A	P
2. Hypocone development on P ³	A/S	D
3. Division of parametacone into two distinct cusps on P ³	A	P
4. Well-developed diagonal crest on parametacone of P ³	A	P
5. Link between protocone and parametacone on P ³	A/W	ST
6. Mesostyle retracted towards cingulum	A	P
7. Size of P ³ relative to equal molars	S	=
8. Elongate P ³	A	P
9. Buccal cingulum on P ³	ST	W
10. Loss, incorporation or suppression of stylar cusps C and D with respect to lophs	A	P
11. Small parastyle on M ¹	P	A
12. Occlusal shape of M ¹	E	SQ
13. Short posterior moiety on P ₁	P	A
14. Paracristid on M ₁	P	R

but incomplete; left I² and L and RI³ are missing; the cranium is in two parts, the division occurring approximately 15mm posterior to the molar rows; the nasals, frontals and palate are incomplete; the basicranium is relatively intact; the posterior region of the neurocranium is missing on each side.

ETYMOLOGY. For the former Vice Chancellor of the University of New South Wales, Professor Michael Birt, who assisted in the collection of specimens and helped meet the cost of preparation..

DIAGNOSIS. Differs from *S. johnnilandi* by: being smaller; having canines; having reduced parastyle and parastylar region on P³ and less elongate P³; having a more central parametacone on P³; having a smaller protocone on P³ that is less distinctly separated from the base of the parametacone; lacking a hypocone on P³; and having steeper protoloph and metaloph faces on M¹⁻⁴. Differs from *Silwabestius* sp. in: being higher crowned; lacking a well-developed parastylar region on P³; and having a reduced posterolingual cingular shelf on P³.

DESCRIPTION. This species is described in so far as it differs from other species of the genus. Incisor arcade poorly-preserved with only the L and R I¹ (both of which are incomplete) and the right I² remaining. Incisors as in *S. johnnilandi*.

Canines small, pointed, on the premaxillary-maxillary suture whereas in *S. johnnilandi* the tiny canine alveoli lie approximately 2mm behind the premaxillary-maxillary suture.

Left cheektooth row badly fractured with a large fissure extending across the buccal margin of M¹, diagonally through M² and across the lingual region of M³, terminating at the anterior base of the hypolophid of M³. Right M¹ fractured diagonally from the anterolingual tooth corner to the posterobuccal tooth corner.

P³ smaller, lacking a distinct cusped parastyle, with parastylar region reduced; vague preparametacrista continuous with the anterior cingulum; parametacone more posteriorly along the longitudinal axis, with postparametacrista more steeply inclined; protocone smaller, less distinctly separated from the base of the parametacone; hypocone absent; protocone without crests.

Upper molars. Lower-crowned, with more extensive wear facets, with more steeply inclined posterior surfaces of the protoloph and metaloph; with a molar gradient not increasing posteriorly.

Ngapakaldia and *Pitikanitia* as outgroup for analysis of the Zygomaturinae due to their plesiomorphic position in the Diprotodontoidea.

CHARACTER ANALYSIS. Fourteen dental characters considered taxonomically useful in zygomaturine intergeneric relationships are employed in a cladistic analysis (Table 4). Selection of characters follows previous phylogenetic analyses by Murray (1990b) and Hand et al. (1993a). Character state polarities (Table 3) were determined by outgroup analysis using *Ngapakaldia* and *Pitikanitia*. Character state polarities for *Nimbadon* were scored only for *Ni. lavarackorum* and *Ni. whitelawi*, for reasons given in the discussion. *Raemiotherium yatkolai* was excluded from the phylogenetic analysis because 13 of the 14 characters are unknown for this species.

A Wagner analysis was performed using the PAUP (version 3.1.1) computer program (Swofford, 1993). Multistate characters were treated as polymorphisms. Character optimisation was performed using both the accelerated (ACCTRAN) and delayed (DELTRAN) transformation algorithms.

CHARACTERS EXCLUDED FROM THE ANALYSIS. For many characters examined from previous phylogenetic analyses, intraspecific and interspecific variation was found to be high. Similarly high variation is characteristic of the Oligo-Miocene zygomaturines *Neohelos* and *Alkwertatherium* (Murray, 1990b). Characters with a high degree of intraspecific variation excluded from the analysis include: the degree to which the parastyle of P³ is posteriorly inclined or 'hooked'; shape of the lingual cingulum on P³; presence or absence of a protostyle on M¹; extent of metaloph reduction on M³⁻⁴; extent of reduction of M⁴. 'Proportional similarity' of P³ as a synapomorphy for a *Plaisiodon*/*Nimbadon*/*Neohelos*/*Kolopsis*/*Zygomaturus* clade, used by Murray (1990b) and Hand et al. (1993a), is a character complex relating to the development of the parastyle, protocone and hypocone. Accordingly, it is not included as a discrete character.

RESULTS. Wagner analysis using the branch and bound algorithm generated a single most parsimonious tree (Fig. 11) involving 23 steps with a consistency index (CI) of 0.880, a retention index (RI) of 0.880 and a rescaled consistency index (RC) of 0.774. The high consistency index probably reflects the limited number of characters used in the analysis. Tree topology was iden-

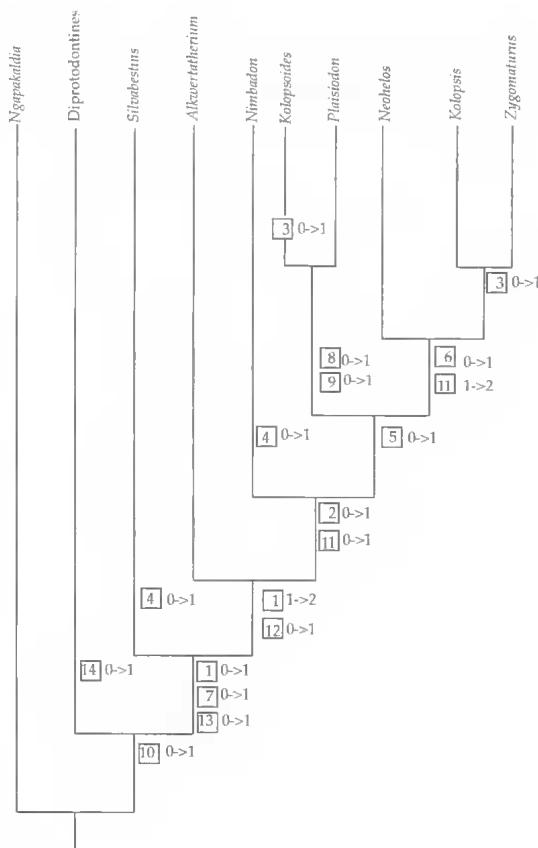


FIG. 11. Hypothesis of zygomaturine relationships, based on dental characters (Table 3) used by Murray (1990b) and Hand et al. (1993) in cladistic analyses of the Diprotodontidae. Apomorphies are represented by boxed numbers. Arrows indicate character state transformations. Symbols: 0, plesiomorphic character state; 1, derived character state; 2, most derived character state.

tical irrespective of whether ACCTRAN or DELTRAN character optimisation was employed.

DISCUSSION

Silvabestius is the most plesiomorphic zygomaturine known with the possible exception of *Raemiotherium yatkolai*. *Silvabestius* is basal to the diprotodontoid radiation. Although similar to the primitive palorchestid *Ngapakaldia* in dentition (Tedford, 1967) and the middle ear, *Silvabestius* is assigned to the Zygomaturinae because it possesses a number of zygomaturine

synapomorphies including a parastyle on P^3 and a ventral alisphenoid tympanic process.

Stirton et al. (1967) and Murray (1990b) suggested that zygomaturines evolved from primitive diprotodontine-like forms in which the parastyle on P^3 was small. Trends in premolar morphology in *Silvabestius* support this hypothesis. Transition from the simple, bicusped diprotodontine P^3 to the plesiomorphic, 3-cusped zygomaturine premolar of *S. michaelbirti* is achieved through expansion of the parastylar region (resulting in a more elongate premolar) and the posterolingual cingular shelf. Subsequent transition to the more typical 4-cusped zygomaturine premolar of *S. johnmilandi* is achieved through development of a distinct parastyle on the enlarged parastylar region and development of a distinct hypocone on the enlarged posterolingual cingular shelf.

Silvabestius is the plesiomorphic sister group to all other zygomaturines (Fig. 9). Plesiomorphic features of the dentition include a poorly-developed parastyle, a poorly-developed hypocone, an undivided parametacone on P^3 , and a well-developed paracristid on M_1 .

Monophyly of Zygomaturinae is supported by: a parastyle on P^3 ; P^3 equal or subequal to the molars in length; and an enlarged posterior moiety on P_3 . The zygomaturine sister-group of *Silvabestius* is united by synapomorphic a moderate to large parastyle on P^3 and square vs elongate molars (in occlusal view). A distinct hypocone on P^3 and a well-developed parastyle on M^1 are shared by *Nimbadon*, *Kolopsoides*, *Plaisiodon*, *Neohelos*, *Kolopsis* and *Zygomaturus*. The latter genera, with the exclusion of *Nimbadon*, is united by a linking crest between the apices of the protocone and parametacone on P^3 . *Kolopsoides* and *Plaisiodon* are united by an elongate P^3 and a weak buccal cingulum on P^3 . *Neohelos*, *Kolopsis* and *Zygomaturus* form a clade rationalised by a mesostyle that is retracted towards the cingulum on P^3 and by a large parastyle on M^1 . *Kolopsis* and *Zygomaturus* are united by a parametacone on P^3 that is divided into two distinct cusps.

Topology of the cladogram (Fig. 9) is consistent with that found in Hand et al. (1993a) and Murray (1990b). However, it differs in the relative positions of species of *Nimbadon*, *Plaisiodon* and *Kolopsoides*. These differences result from the exclusion of certain characters used in previous analyses which are of low taxonomic value. A hooked or posteriorly inclined parastyle on P^3 has been used by Murray (1990) and Hand et al.

(1993a) as a synapomorphy uniting *Plaisiodon* and *Nimbadon*. In this analysis the character was found to be highly variable and hence of low taxonomic value. No special affinity was found between *Nimbadon* and the *Kolopsoides/Plaisiodon* clade. Further, Hand et al. (1993a) united *Nimbadon*, *Plaisiodon*, *Neohelos*, *Kolopsis* and *Zygomaturus* to the exclusion of *Kolopsoides* by the similarly proportioned P^3 . This character was excluded from the current analysis because it was found to be dependent on the degree of development of the parastyle, protocone and metacone on P^3 .

The position of *Kolopsoides cultridens* within the Zygomaturinae is difficult to determine, partly because of the paucity of knowledge about late Miocene diprotodontoids. Stirton et al. (1967) suggested that *K. cultridens* is most closely related to *Kolopsis* on the basis of a divided parametacone on P^3 . Flannery (1994) suggested that all New Guinea diprotodontids, including *K. cultridens*, are closely related and probably stemmed from a *Kolopsis*-like ancestor. *K. cultridens* is here linked with the late Miocene *Plaisiodon centralis*, from the Alcoota Local Fauna, a relationship first proposed by Archer (1984). If this relationship is accepted a divided parametacone has developed within the Zygomaturinae in the *Kolopsoides/Plaisiodon* lineage and again, convergently, in the *Neohelos/Kolopsis/Zygomaturus* lineage. Homoplasious division of the parametacone into 2 distinct cusps would then have developed during the late Miocene perhaps in response to increasing dryness. With plant materials becoming less succulent and more abrasive, there may have been strong selective pressure on all lineages to increase molariform features as well as the surface area of premolars.

We suggest that *Nimbadon scottorum* is more appropriately assigned to *Neohelos*. Features of the dentition that align *Ni. scottorum* with *Neohelos* are: larger, squarer molars; more robust cingula on the cheekteeth; greater parastyle development on M^{1-2} ; a relatively erect parastyle on P^3 ; and an anterolingual crest extending from the parametacone apex that meets a buccal crest from the apex of the protocone (a feature common in species of *Neohelos*) rather than continuing on to meet the anterolingual cingulum as in *Ni. lavarackorum* and *Ni. whitelawi*. Material referable to a small species of *Neohelos* from Riversleigh's System A Local Faunas, and forms intermediate between this small *Neohelos* species and *N. tirarensis* from Riversleigh's System B Local Faunas, are relatively indistinguish-

able in terms of morphology and dimensions from the Holotype and only specimen of *Ni. scottorum*, QMF23157. Consequently, character polarities for species of *Nimbodon* in this analysis were determined using *Ni. lavarackorum* and *Ni. whitelawi* only.

Similarities in dentitions of *Silvabestius johnniliandi* and *Nimbodon lavarackorum*, both from Riversleigh, and *Ni. whitelawi*, from the Bullock Creek Local Fauna include: molar dimensions; structure of the parastylar region; protocone; hypocone; buccal cingulum; and anterolingual parametacone blade on P^3 . The last feature was suggested (Hand et al., 1993a) as an autapomorphy for *Nimbodon* but it is variably expressed in *Neohelos* and well-developed in *Silvabestius*. Dentitions of *S. johnniliandi* and *Nimbodon* differ mainly in the degree of development of the parastyle on P^3 and the extent to which it is separated from the base of the parametacone. Plesiomorphic features of *Nimbodon* include a small parastyle and undivided parametacone on P^3 , elongate vs relatively squarish molars, and a well-developed paracristid on M_1 .

Murray (1990b) suggested that *Nimbodon* may be a basal zygomatuline with affinity to *Neohelos* and *Plaisiodon*; he suggested 2 minor zygomatuline lineages, *Nimbodon*, *Neohelos* and *Kolopsis*, united largely through plesiomorphic features and *Alkwertatherium*, *Plaisiodon* and *Kolopsoides*, united through phenetic similarities of the dentary and lower incisors. He also suggests that these lineages may be united through common ancestry in *Nimbodon*. In our analysis *Nimbodon* occupies a more plesiomorphic position than in other analyses.

Some doubt remains about whether *Raemerotherium yatkolai* is appropriately included within Diprotodontidae. Rich et al. (1978) noted that it exhibited no apomorphic character states that precluded the possibility that it was a primitive macropodoid but, equally, neither does it exhibit any character states that are undoubted macropodoid synapomorphies. The relative phylogenetic positions of *Silvabestius* and *Raemerotherium* cannot be resolved until upper dentitions are discovered for the latter. Differences in the lower dentition of *S. johnniliandi* compared with *R. yatkolai* include: it is larger; lophids on the lower molars are less anteriorly convex; the anterior moiety of M_1 is broader; the premetacristid of M_1 is better developed as is the anterolingual basin at the anterior base of the protolephid; the protostylid (Rich et al., 1978) at the buccal base of the protoconid on M_1 is absent; and the pro-

tolophid on M_1 is more posteriorly inclined. Both species exhibit an $M_1:M_3$ ratio (equivalent to $M_2:M_4$ in Rich et al., 1978) approaching 1, a condition regarded as primitive among diprotodontoids. There are no apomorphic features of the lower dentitions that enable either to be regarded as unambiguously more plesiomorphic than the other.

Silvabestius johnniliandi is derived relative to *S. michaelbirti* as evidenced by the following features of its P^3 : a more distinct parastyle; a larger, lobate parastylar region; a better defined preparametacrista; and a small but distinct hypocone. The relative position of *Silvabestius* sp. is more difficult to determine because of poor preservation. However, the following features of the dentine core suggest that *Silvabestius* sp. is structurally intermediate between *S. michaelbirti* and *S. johnniliandi*: parastylar region more extensive than *S. michaelbirti* but reduced in comparison to *S. johnniliandi*; hypocone absent in *S. michaelbirti*, a more extensive posterolingual cingular shelf in *S. sp.*, a feature that anticipates the development of a hypocone in *S. johnniliandi*. *Silvabestius* sp. has no autapomorphic features in the dentition that would preclude it being the ancestor of *S. johnniliandi*. Alternatively, *Silvabestius* sp. may represent an extreme end of an *S. johnniliandi* morphocline. If this is the case, the simple dental structure of *S. michaelbirti* and the absence of any autapomorphic features of the dentition, suggest this species may represent the direct ancestor of *S. johnniliandi* and the structural antecedent of all other zygomatulines.

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